KANO *The Last Ape* *Pygmy Chimpanzee Behavior and Ecology* STANFORD

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TAKAYOSHI KANO

Translated by
Evelyn Ono Vineberg

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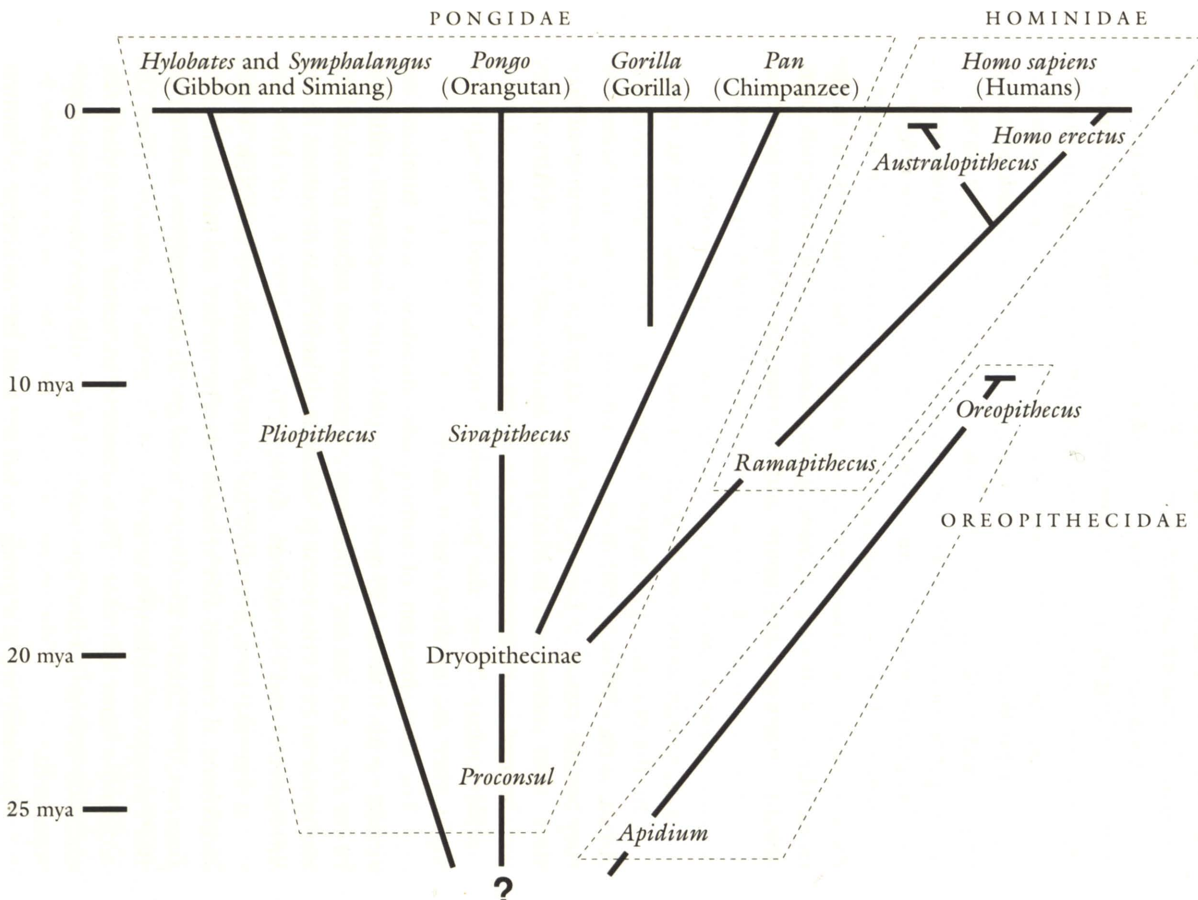
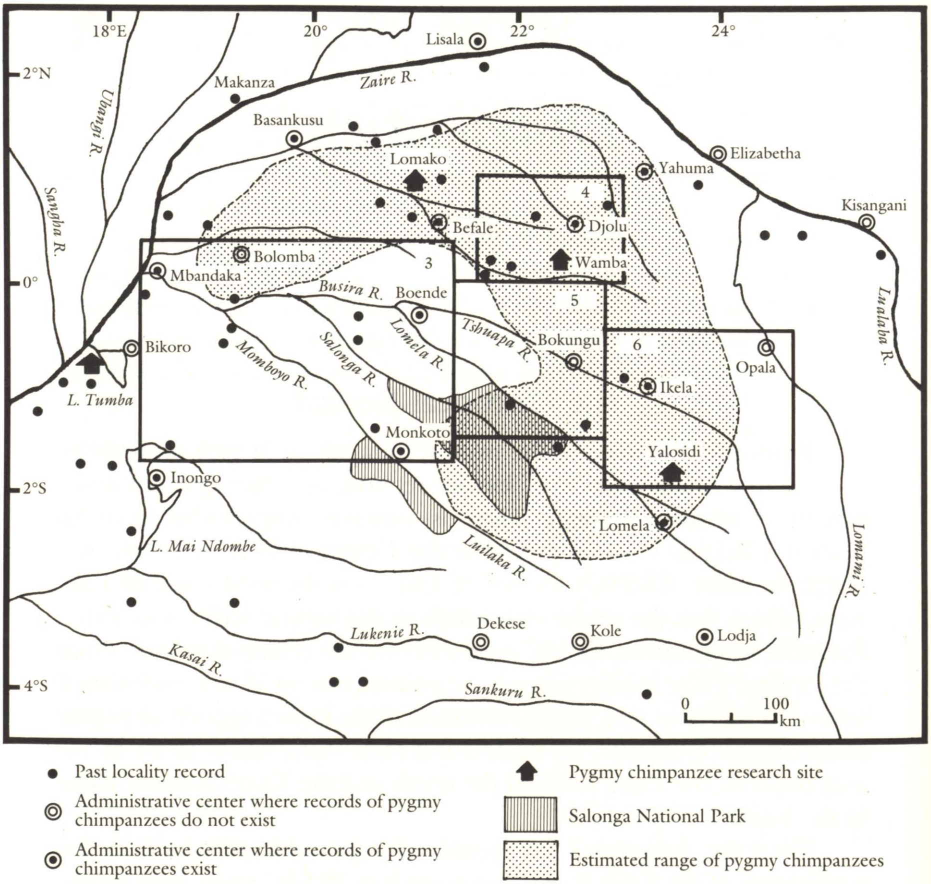


Figure 1. Classical hominoid family tree (after Simpson, 1963; Schultz, 1966).



Map 2. Distribution of pygmy chimpanzees (adapted from Kano, 1984a; by permission of S. Karger AG, Basel) This map is based upon information gathered by the author in 1973. The present distribution of pygmy chimpanzees is probably smaller. The large rectangles indicate the boundaries of Maps 3–6.

from local inhabitants, and such purchases identified a locality as a regional collection and distribution area. It must have been at these local, central towns where collectors in the past could easily find their specimens. Antelopes, monkeys, birds, and various other animals were brought to local trading centers from distant villages, where they were sold in the market, not only as pets but as food. Chimpanzees also were eaten in many regions. Therefore, it is no wonder that many of the locality rec-

CHAPTER FOUR

Food and Nutrition

The Variety of Foods

Primates, in general, are regarded as mainly plant-eaters. Among herbivores, there are monophagous species, such as koalas, who are said to eat only the leaves of eucalyptus. Primates, however, will not tolerate such a monotonous diet. No matter at which primate we look, it probably utilizes a large number of plants as food.

Plants germinate, their leaves grow thick, their flowers bloom, they bear fruit, and they scatter their seeds. When the appropriate season comes, some plants drop their leaves while other plants die back. In this way, plants variously change their guise in response to the respective phenology. This is the same for vegetation of regions that have four seasons, for vegetation when there is a dry and a rainy season, or for vegetation in limited humid tropical regions where climatic change is barely visible.

Primates eat not only many species of plants but various parts of the plant as it changes form in response to the season. By so doing, primates were able to adapt well to the rich complexity of the plant world (especially the forest) where "diversity" is the special feature of their food.

Plants impart a completely different taste depending on the species and the part eaten, as do different meats. It has been said that primates are animals with the most developed sense of taste. That is probably because it was necessary to identify the flavors of various species of food.

The food list of pygmy chimpanzees recorded at Wamba consists of 147 items (Appendixes 1 and 2) and the number will probably continue to increase as we gather more data. Although pygmy chimpanzees subsist primarily on plant food, including the flesh of fruit, seeds, sprouts, leaves, flowers, bark, stems, pith, roots, and mushrooms, they also eat small mammals (flying squirrels, etc.), insect larvae, earthworms, honey, eggs,

A pygmy chimpanzee feeding on *Dialium*.

and soil. Fruits (pulp, seeds) occupy 57% of the whole list and probably form the core of their diet when considering only food type.

A special problem that continues to bother researchers in primate ecology, however, has been how to quantify actual intake. Up to the present, the methods traditionally used to investigate intake are (1) estimation according to the duration of feeding, (2) estimation using the quantity of the contents of their feces, and (3) estimation by use of both sets of information. Each method has perplexing shortcomings.

The quantity of food that is taken in during a set feeding interval—intake efficiency—differs greatly depending on the degree of enthusiasm or hunger. Also, even if the enthusiasm is the same, the intake efficiency may differ depending on the nature of the food. As an example, compare how someone eats a large football-size fruit with plenty of flesh attached to how one eats small fruits having skin that must be removed diligently, piece by small piece.

Differences in observation conditions are also important. For example, when chimpanzees are eating high in a large tree, frequently several individuals are in the field of vision simultaneously for a long time. When they are feeding on the ground in dense forest undergrowth, how-

ever, occasionally one individual will be visible and then disappear. Thus, we cannot know exactly the absolute quantity, nor the relative quantity, of food consumed from just the apparent feeding duration.

By studying the contents of feces, we can compensate for some of the weaknesses of direct observation since the results of feeding activity over a long time are compressed. This kind of analysis is not affected by differences in observation conditions, but there are defects. Seeds that have been eaten whole together with their flesh can be readily detected in the feces. But fecal analysis is exceedingly difficult to undertake when seeds or things crunched by teeth and eaten (for example, beans), stems/stalks, leaves, pith, and fibrous parts of the plant body are eliminated as fragments of indigestible parts. In all instances it is certainly difficult to estimate the quantity of plants eaten, even if we can identify what was eaten. Seeds that are too large and that may be discarded after consuming the flesh will not be detected by fecal analysis.

In conclusion, to figure accurately the amount of food consumed by a species, it may be necessary to follow one individual all day, and to do nothing else but diligently record how much and what it eats. In order to do that, the focal individual must always be kept within the field of view. In the dense forest of present-day Wamba, this is only a hope.

The method I finally used to estimate feeding proportion (the percentage occupied by each food item relative to the whole quantity of food consumed) was a rough compromise. When I discovered an individual who was eating food A, I scored one point for that food. If two individuals were simultaneously eating that food, two points were scored. The scoring occurs from the beginning of observations and continues every time there is a lapse of at least 30 minutes. For example, at 10:00 A.M., one individual is feeding on A (one point); at 10:34 A.M., two individuals are feeding on A (two points); and at 11:20 A.M., three are feeding on A (three points), providing a total of 6 points scored for A. If, on the way, the focal animal samples a different food B, I take that as a new starting point. For example, if an individual who has eaten A eats B and then returns to A within 30 minutes, I will score two points for A and one point for B.

Fecal analysis is handled independently. Feces that are found are wrapped separately and carried back to the research base. After measuring the weight of just the fecal calyx (measurable up to 200 g), we put it in a sieve and wash it in water. We wash away the pasty part; spread what remains on top of a paper; and separate similar kinds of food residues

Table 12. Feeding proportions (percent) (Kano and Mulavwa, 1984)

Food	Direct observation 11/1/75–2/10/76	10/9/76–12/31/76	10/20/77–2/10/78	10/21/81–2/28/82	Mean	Fecal analysis, 11/1/81–2/28/82
Fruits						
Arboreal	84.3	90.7	79.6	79.1	83.4	86.8
Ground	0	0	0	0	0	6.3
Total	84.3	90.7	79.6	79.1	83.4	93.1
Leaves						
Arboreal	13.4	9.1	15.9	11.8	12.6	3.7
Ground	2.3	0.2	1.7	6.0	2.6	2.0
Total	15.7	9.3	17.6	17.8	15.2	5.7
Animal foods	—	—	2.8	3.1	1.5	1.1

(seeds are abundant), concentrating them into piles. We estimate the quantitative ratio by eye.

The results of direct observations and fecal analyses are displayed in Table 12. As mentioned previously, differences based on the special characteristics of the two methods are apparent, but the obtained ratio of food intake by pygmy chimpanzees at Wamba is as follows: fruits, including seeds, 80–90%; fibrous foods or leaves, 10–20%; other (animal material, etc.), several percent. Thus, when we consider the species of food and the quantity consumed, the most important food is fruits.

Principal Foods and Seasonal Changes

Although we could say that a special feature of the chimpanzee diet is its diversity, when we look at feeding time, we find that they are not taking in many different foods. The average number of food items recorded per day by direct observation is 2.0 types (range, 0–9 types; *N* [number of observation days] = 302 days) and by fecal analysis, it is 6.0 types (range, 1–12 types; *N* = 140 days).

The number of food types that are recorded by direct observation increases with the length of observation time. In fecal analysis, when the number of examined feces reaches 5 or 6 samples, the number of food types does not increase beyond that. In other words, the examination of feces may be a method that surpasses direct observations to assess diet quickly.

When we investigate the number of kinds of foods per month, we find similar tendencies when using the two above-mentioned methods. The number of food types recorded by direct observation is 7–29 types per month (range of time of direct observations, 4.1–108.7 hours; number of months = 18). As the observation time increases, we obtain a curve that increases gradually (Fig. 9). The extreme value of this upwardly curved line is probably an approximation of the actual number of species of foods consumed per month. From Fig. 9, we estimate that it is probably about 40 species.

On the other hand, from fecal analysis, we get 22–27 species per month (range of number of feces, 192–328 samples; number of months = 4). Variation depends on the number of months and the number of fecal samples, but is slight. Consequently, we decided that 200 individual scats was a sufficient sample from which to obtain the upper limit for the number of food species per month as determined by fecal analysis. Because of the defects of fecal analysis that make detection difficult for some foods, this upper limit must be lower than the true value.

Although many foods are included in the diet, this does not mean

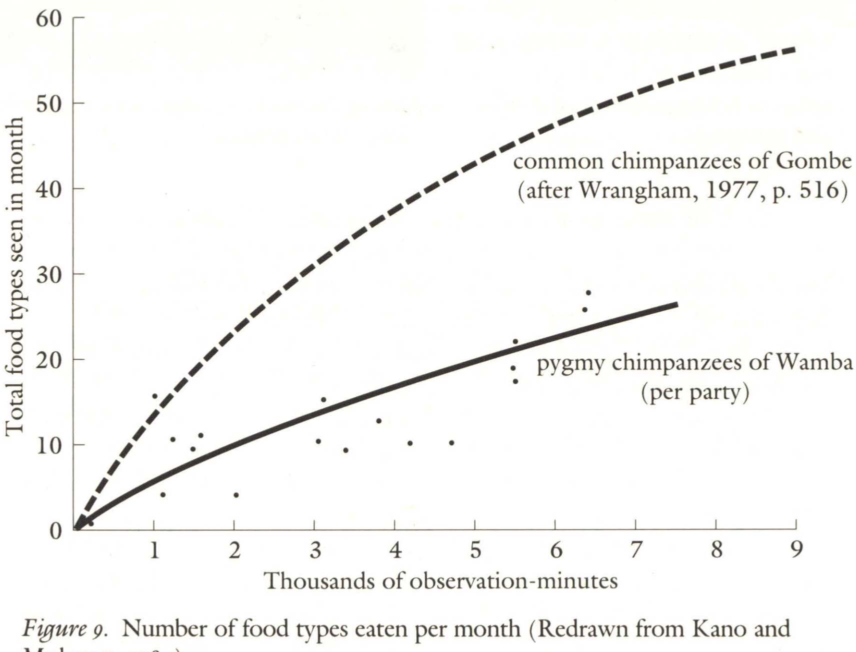
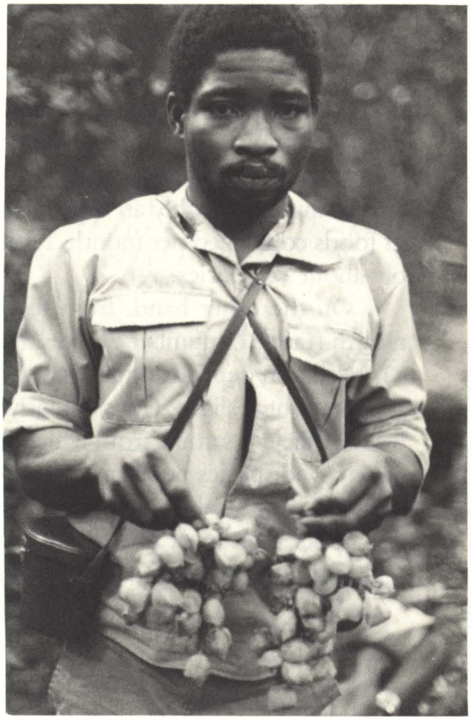


Figure 9. Number of food types eaten per month (Redrawn from Kano and Mulavwa, 1984).

Wamba villagers holding clusters of *batofe* (*Landolphia owariensis*).



One of the trackers, Nkoi, with *ntende* fruit (*Pancovia laurentii*).

that each of these foods has equal importance. If you look at a one-month unit, one species of food alone may occupy an average of 50% of the total ratio of food taken. In addition, the ratio of consumption of the top-ranking six food items, taken together, amounts to 90% of all food stuffs. Pygmy chimpanzees rely on and survive on a small number of food items of what should be called "staple foods."

In general, fruits ripen during a certain fruiting season, but these seasons differ in length. Therefore, the food items that serve as staples fluctuate according to the fruiting season. Some tropical fruits differ from Japan's seasonal fruits by lacking a clear annual fruiting cycle. Moreover, various tree species have independent phenological cycles that complicate matters. For example, the fruit of a woody vine of the Apocynaceae family called *batofe* (*Landolphia owariensis*) normally begins to ripen in about August and becomes a staple food of pygmy chimpanzees at that time; but at the end of September, the fruit disappears. Bumper crops of

batofe occur in irregular cycles at an interval of from one to three years. In those years, the fruiting season lasts until the end of December.

The majority of tree species that have a vegetation phenology like that of *batofe* bear fruit in large quantities once every several years, according to observations in the Zaire Forest. Because many of the species, like *batofe*, are not abundant, they are significant as food only once every several years. In the Wamba forest, there are at least four species of *Dialium* (locally called *keke*, *laka*, *elimilimi*, and *boleka*); they have a stable annual cycle of fruit production between October and February. Every year *Dialium* spp. as a group provide the pygmy chimpanzees of Wamba with very reliable staple foods. By contrast, at Yalosidi, which is 220 km south of Wamba, the annual production of *Dialium* spp. (locally called *lokake* and *elimilimi*) appears to fluctuate a great deal. In November 1973, when I first visited there, *Dialium* fruit was the predominant food of the chimpanzees. According to what I heard later, that fruiting period lasted until about March of the next year. However, during my subsequent research from November 1974 to February 1975, not one morsel of *keke* fruit was seen. Pygmy chimpanzees must survive while faced with this kind of unstable fruit production, and consequently, their food repertoire must be large.

I divided the foods of the pygmy chimpanzee into three grades in accordance with their level of importance, and each month was divided into three 10-day periods. Staple foods were those that constituted more than 30% of the intake ratio in at least one period; semi-staple foods were those that accounted for 30–10%; and supplementary foods, those that supplied less than 10%. In a total of 45 periods of research, the foods that became semi-staple or staple foods, at least once, consisted of an overwhelmingly great number of fruits (23 species), the leaves, stems, and pith of eight species of fibrous foods, and two species of animal food products.

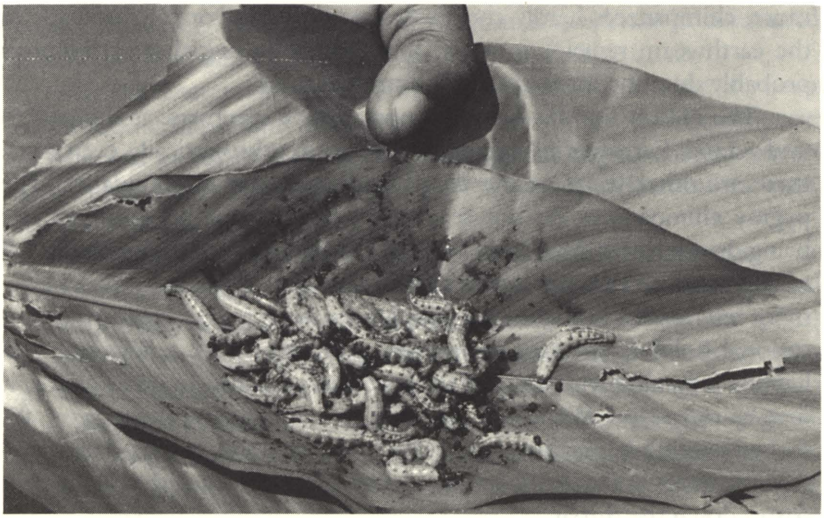
Almost all of the arboreal species that have become principal foods are large trees or woody vines with fruits. For example, trees of the genus *Dialium* are emergents (large trees whose crowns jut out above the line of the tropical rain forest's uppermost stratum). In the peak fruit-bearing period, a large group of 40 pygmy chimpanzees may visit the same tree several times. The woody vines of *Landolphia* spp. are similar to *Dialium* spp. in their pattern of fruit production. The vines climb up around large forest trees and produce numerous fruits the size of oranges on the crown surfaces. Thus, the principal foods of pygmy chimpanzees have the special feature of being produced in large quantities in one food patch. If this were not so, they would not be staple foods.

Among fibrous food items, the most important food types are the shoots of herbs of the family Marantaceae. At Wamba, there are more than ten species of Marantaceae, and all of them send up a slender sprout. Chimpanzees strip off the hard outer husk and eat the tender, white leaf-roll inside. Shoots of *Megaphrynium macrostachyum* and *Haumania liebrechtsiana* are the most preferred. The shoots of the former are called *beiya* or *beiye* and are also consumed by the villagers, who consider them excellent vegetables. *Beiye* is the main objective of gathering forays that the women of Wamba make every several days. Collected in large quantities and brought back to the villages in shoulder crates, *beiye* can be eaten raw, but if boiled with fish and meat, it has an indescribably delicious flavor; the crunchiness is also good. If we compare it to the vegetables of any other country, I believe it would be considered first-rate. That there is no *beiya* in Japan is truly regrettable.

The shoots of each species of Marantaceae including *beiya* are not seasonal and are frequently fed on by chimpanzees. Because the shoots are scattered uniformly over a wide area, however, they are inconspicuous when fruit foods are abundant. The fibrous foods become prominent as principal foods during the dips between the fruiting seasons of staple fruits.

The larvae of a hesperiid butterfly called *tohilihili* is one of the pygmy chimpanzee's favorite animal foods. These green caterpillars, about half the size of a silkworm, infest the *botuna* (*Cynometra hankei*) trees starting in the middle of December, after a continuous period of scant rain lasting up to one and a half months. During this period when you walk in the forest, you can hear a sound like that of drizzling rain striking a roof, but it is the sound of the caterpillars' fine droppings falling from the large *botuna* trees and hitting the leaves of the undergrowth. Pygmy chimpanzees voraciously eat caterpillars during this period, but the *tohilihili* season lasts, at the most, from only one week to ten days.

Another animal food item is the earthworm. Two species of earthworm are eaten: one lives in the forest floor of *bombongo* (*Gilbertiodendron dewevrei*) groves and the other lives in swamps. The chimpanzees dig and search for them in the dirt or mud using only their hands. In swamp conditions, they dig diligently for earthworms, sometimes foraging slowly for as much as three to four hours. Because this kind of feeding is slow, the amount of time spent feeding is high, but the intake efficiency is very low. In my observations, a male chimpanzee who was carrying something in his mouth took, on average, one every 25 minutes in the swamps and one no more than every 2.5 minutes in the *bombongo* grove. Further-



Caterpillars or *tohilihili* (the larvae of a hesperiid butterfly), eaten by pygmy chimpanzees and villagers.

Millipedes were reported to be eaten by pygmy chimpanzees at the American field site, Lomako.

more, chimpanzees hardly chew when eating earthworms; the shape of the earthworm remains intact in the feces. We think that earthworms probably do not contribute much nutrition at all.

The reason for this kind of unproductive enterprise is difficult to understand. Earthworm-digging is performed enthusiastically, even when there are other foods of the *batofe* fruiting season in abundance. The pygmy chimpanzees do not search out earthworms because they are being driven to eat them from hunger. Instead, they are undoubtedly full enough and, in fact, eat earthworms when there is leisure time. The activity resembles a household of people who leave for the coast on an occasional holiday, amusing themselves gathering shells at low tide and happily returning with a cupful of short-necked clams. In other words, it may be recreation. When you see the figure of a pygmy chimpanzee absorbed digging in the dirt, that is what you may think. It is hard to accept that the merit of this habit is the slippery sensation when the earthworm passes down the throat.

Recently, there was a television report that in the United States, earthworms raised as fishing bait are becoming a popular item for people to eat. Adults or even children, at mealtime, merrily picked out wiggling earthworms, heaped in a bowl, and put them in their mouth. I was dumbfounded, but I was reminded of the earthworm-digging of pygmy chimpanzees. Earthworms may prove to be unexpectedly good to eat.

Taste

The fruits of *Dialium* normally begin to ripen about October, and at this time, the pygmy chimpanzees may start to eat them. As long as the *batofe* fruits last, however, *Dialium* is not consumed much. Consequently, once, after several years when there was an abundance of *batofe*, *Dialium*-eating was delayed until December. When the *Dialium* season passes, the season of *ntende* (*Pancovia laurentii*) begins, extending from the end of January to the beginning of February. Usually, *ntende* begins to ripen shortly after *Dialium* is finished, but in the year when there was a delay because of the abundance of *batofe*, *ntende* began to ripen during the fruiting season of *Dialium*. At that time, the pygmy chimpanzees left the *Dialium* to feed on *ntende*. Then when *ntende* was finished, they returned to the *Dialium* that was left.

In an average year, *Dialium* is an important food that is the most stable of the staple foods of pygmy chimpanzees. Its relative value de-

creases, however, when the fruits of *batofe* and *ntende* can be consumed. Clearly in chimpanzees, as in humans, taste preference exists.

We think several factors determine food preferences. First, the flavor of the food is important, as it is in the three previously mentioned species of principal foods. But among the foods that the pygmy chimpanzee enjoys eating, many are sweet and sour. The strong inclination for sweet flavors is assumed by humans.

We think that the relative difficulty of the feeding process, the intake efficiency, and related matters also influence preferences. *Dialium* fruit has a stronger sweet taste than the fruit of *batofe* and *ntende*, and it has a refreshing flavor. There is no reason for human judgment to be the same as the chimpanzee's, but when I asked people to make a taste comparison, they said *Dialium* was the most delicious. Compared with *batofe* and *ntende*, *Dialium* fruit has one disadvantage as a good food. Eating it is a nuisance; it is small and the edible part is concealed by a brittle and fragile skin. The work of processing the fruit is tiresome and time consuming. Accordingly, intake efficiency must be low.

There may be other reasons for *ntende* being preferred over *Dialium*. The *ntende* trees in the forest are filled with enormous orange clusters of fruit, which ripen quickly in one to two days. However, the season also ends quickly. Within ten days to two weeks, the fruits completely vanish. As expected, the appetites of chimpanzees and monkeys do not diminish at this speed. At the end of the fruiting season, many *ntende* fruits fall to the ground, and although satisfying in their sweet and sour fragrance, some are left to rot. Eating *ntende* is a race with time.

Dialium, on the other hand, is a long-lasting fruit, with a fruiting season that lasts several months. Some fruits fall to the forest floor, and the outer covering becomes black. But even if they grow moldy, the interior seems to stay edible. I was amazed to see pygmy chimpanzees carefully push aside fallen leaves and select *Dialium* fruit in this condition, one by one, as we might search for mushrooms. With the covering removed, the flesh within certainly does not appear much changed from when it was attached to the branch of the tree. I have not, however, had the nerve to sample the food. Owing to the length of the fruiting season of *Dialium*, it seems like an exaggeration to say that the pygmy chimpanzee exhibits food selection, but it is possible.

Preferences toward foods change even within one day. After arising in the morning, pygmy chimpanzees have fruit as their primary food objective. Then from noon, the sprouts of herbs (Marantaceae), tree leaves,

and other fibrous foods are consumed in large amounts. The pattern of consumption in which fibrous foods are used relatively late in the day has been observed also in the common chimpanzee.

This pattern is explained by the existence of poisonous substances, called toxic secondary compounds, in the body of the plants. Plants, which are immobile and suffer from the free attacks of mobile animals, have produced toxic secondary compounds to defend themselves. Because plants must defend themselves throughout the year, especially in the tropical rain forest where seasonality is limited, most plants apparently have these poisonous secondary compounds. The toxic secondary compounds are not found in nectar and pollen. The reason for their absence from pollen is unclear, but nectar was adapted originally for being eaten by animals. Fruit, another part that is meant to be eaten, also contains toxic secondary compounds; there is a need to single out the animals that are seed dispersers. Naturally, there are more toxic secondary compounds included in other parts of the plant body (Janzen, 1975).

Chimpanzees prefer young leaves and sprouts as fibrous food. Among a variety of poisonous secondary compounds, the representatives included in young leaves and sprouts are alkaloids. The quantity of alkaloid within plant bodies has its highest value in the early morning, and declines during the day. Following its daily cyclic rhythm, toxicity starts to accumulate again in the evening. Chimpanzees select foods by adapting to this physiological rhythm of plants, inferring it by some mysterious means.

Foods must be considered from two standards—availability and preferences (we cannot deny that chimpanzees have food preferences). Foods that are found in great quantity and are highly preferred often become staple foods. The feeding habits of chimpanzees may be sustained principally by these foods. Foods that are quantitatively scarce but highly preferred are potentially important foods. If environmental changes favor a large yield of them, they might be adopted by pygmy chimpanzees as staple foods.

The majority of the foods, reaching 147 species in the pygmy chimpanzee, are not highly preferred and are thought to be rather unimportant. Up to the present, most of them have shown up only infrequently in the growing body of research reports. Moreover, all of the foods that will be added to the food list in the future will certainly be "snack"-like items. Snacks, however, are not limited only to a supplementary role in the diet of chimpanzees. They may also be a reserve for coping with repeated environmental fluctuations. In the distant future, some hundred or thou-

sand years from now, the chimpanzee's habitat may be quite different from what it is today. The greater their food repertoire is, the greater will be their chances of survival.

Food Culture

Previously, I emphasized the uniform nature of the composition of the Zaire Forest. Reflecting this uniformity in vegetation, many major foods are common over a wide range. At Yalosidi, the fruit of *bondora* (*Trichosypha ferruginea*) and *bofambu* (*Gambeya lacourtiana*) are often eaten (see Appendix 3 for complete list of plant foods at Yalosidi). At Lomako also, the fruit of *bofambu* seems to be an important food. At Wamba, however, neither is eaten. These regional differences reflect the availability of foods. That is, in the forests of Wamba, these tree types do not exist or they are exceedingly scarce.

Among wild plants, the emergent plant *Ranalisma humile*, called *ikora-yokuwa* at Yalosidi, is an example of an item that is used or not used depending on the region, even though it exists everywhere. The Zaire Basin does not produce rock salt, and long ago, people boiled down this grass and obtained *engange*, a salt substitute. *Ikora-yokuwa* occurs abundantly in the swamps of Yalosidi, and pygmy chimpanzees regularly visit the swamps and eat this grass during periodic fruit shortages. At Wamba, the same grass grows thick on the mud floor of the relatively shallow, wide stream of Bokela. The pygmy chimpanzees at Wamba, however, go there to search for worms; they do not touch the grass.

Regional differences are more apparent in animal foods than in plant foods. At Lake Tumba (Horn, 1980), Lomako (Badrian, Badrian, and Susman, 1981), and probably Yalosidi, termites are on the pygmy chimpanzees' menu, but at Wamba, there is no evidence of this whatsoever. In the forest, one can often see a large millipede, the thickness of a finger and 20 cm long, crawling silently. People of the Mongo tribe call it *kongori* and abhor it as a taboo, a messenger of Satan. However, Badrian, Badrian, and Susman (1981) report that the pygmy chimpanzees of Lomako ate these millipedes frequently at a certain time in 1979. At Wamba, this has not been seen. In 1981, when I met Noel Badrian in Boende and asked him directly, he answered that the Lomako chimpanzees ate the millipedes only in that year. Since then, they had stopped eating them, even though large millipedes are available every year and every season. I wonder if pygmy chimpanzees also have fads in food.

In general, pygmy chimpanzees at Lomako consume more varied

animal foods than at Wamba. At Lomako, snake and other vertebrate animal bones and insect legs and wings often are eliminated in their feces. Recently, N. Badrian and R. K. Malenky (1984) reported that a blue duiker was caught and eaten. As far as mammals are concerned at Wamba, only the bones and a piece of fur of a flying squirrel were found several times in feces. Earthworms, however, which have become relatively ordinary food at Wamba, are not reported as food at Lomako.

The repertoire of animal foods is narrower than that of plant foods. This narrow breadth and the local discrepancies in the animal food repertoire indicate to me that the consumption of animal foods occurred later in the history of the pygmy chimpanzee line. Although regional differences in food habits, called "food culture," certainly exist, clarification must await further progress in research both within and outside the region of Wamba.

Even among the five unit groups residing in the forests of Wamba, we see differences with respect to several foods that are limited by conditions of availability. For example, a principal research focus at Wamba in the early days was B-group. Suehisa Kuroda planted a sugarcane field in B-group's range, but it was completely disregarded by the chimpanzees. In the end, it was raided by elephants. A sugarcane field was also planted in E-group's range, however, and after the sugarcane ripened, the chimpanzees of E-group settled in the field and did not leave until they had consumed all of it. The reason for this difference is clear. Sugarcane has been cultivated in this general region for a fairly long time, but only on a small scale—a little bit in people's backyards, yielding an insignificant amount. Nevertheless, the home range of E-group extends over both sides of the road leading from Yaenge hamlet to Yokosi hamlet, and along that road are intermittent rows of houses. Thus, E-group chimpanzees have many opportunities to encounter the edges of sugarcane fields when they cross the road. On the contrary, B-group's home range extends toward the east from Yaenge and also enters between the road, but on this road there are no houses and consequently no sugarcane fields.

Pineapple presents the same kind of situation as sugarcane. Pineapple is also a foreign cultigen, but it so excels in propagative properties that feral pineapple has gone rampant and spread out into the secondary forest of fallow land. Consequently, pygmy chimpanzees of E-group and of B-group take pineapples as food.

Apparently, pineapple is a more desirable food than sugarcane to the members of E-group, because when sugarcane and pineapple are served simultaneously, pineapple is preferred. When P-group came to feed,

however, an interesting thing happened. P-group was divided into two kinds of individuals: ones who dashed toward the pineapples, carrying them away in both hands and fleeing as if afraid of having plundered them, and ones who, quite unconcerned, left with only sugarcane. The individuals who took pineapples were all young parous or nulliparous females, and thus were individuals thought to have recently transferred into P-group. The home range of P-group overlaps broadly with that of E-group, but the former does not extend into the region of the left bank of the Lokuli River where pineapples grow wild. Therefore, the principal members of P-group are unfamiliar with pineapple. By contrast, young females, when they were juveniles in another group or during their adolescent wandering period, had sufficient possibility of coming into contact with pineapple.

Pineapple and various foods other than sugarcane were provided at the feeding site. Remains of small animals and meat did not attract the interest of pygmy chimpanzees at all. Similarly, a live blue duiker and chicken evoked no reaction, except perhaps fear or a threat. Many cultivated fruits were also completely ignored. Only chicken eggs elicited a response resembling, to some degree, that to pineapples. Of 50 individuals who encountered the eggs, 12 carried away one or two. Among those 12, at least 4 individuals bit into, broke open, and ate an egg; the other 38 individuals completely disregarded the eggs. Because the individuals who showed interest in eggs included a variety of age-sex classes such as adult males, middle-aged to old females, and young females, this situation differs from that involving pineapples in P-group. In the case of the eggs in E-group, behavioral differences suggest individual differences in food preferences but not differences between groups.

The females that did not take pineapples, those females past middle-age in P-group, present a problem in understanding the dietary habits of the pygmy chimpanzee. Those females must have been born and raised in a group other than P-group, and some of them must have eaten pineapple while they were young in that group. Those females, who were in their middle years while living in P-group, did not seem to remember pineapples, even though they carried the flavor of home. Because the feeding habits of pygmy chimpanzees are based on this kind of shaky memory, an item may remain in the memory as "food" only if an individual is re-exposed to it within an appropriate interval. In the event that the environment changes, the old food may be forgotten. At such a time, having a wide "range of diet" may provide an important basis for survival. The ability to exploit new, unfamiliar foods may also be important.

The pygmy chimpanzee's tolerance of new food resources may be assessed by how they have accepted newly introduced cultigens (especially fruit-bearing ones). On the basis of my extensive survey, in the regions where pygmy chimpanzees have access to sugarcane, they do eat it. There is, however, not much information from regions other than Wamba about pineapple. Banana, papaya, mango, avocado, sweet oranges, and several other species of fruits are widely cultivated in the Zaire Basin, but there is no evidence that pygmy chimpanzees eat them. Papayas were offered repeatedly to the E-group chimpanzees at the feeding site, but they were ignored, except on one occasion when a young female bit and discarded one after carrying it a short distance. Bananas, which also were offered several times, were completely ignored by all adults; only juveniles approached and sniffed them, without sampling, and only on a few occasions.

The fruit of oil palms in the Zaire Forest is probably one of the easiest cultivated foods for chimpanzees to obtain. Since the early 1920's, when oil palms were introduced into the Zaire basin, they have rapidly spread and now predominate in many secondary forests. Although oil palm fruit is one of the most preferred foods of cercopithecoid monkeys (mangabeys and guenons) in the Zaire basin, there is no evidence, at Wamba or other regions, that pygmy chimpanzees eat oil palm fruit. For whatever reason, pygmy chimpanzees seem to be conservative in exploiting new food resources.

Nutritional Value

Vitamin C. In general, vertebrates more advanced than amphibians can synthesize vitamin C (ascorbic acid). In amphibians and reptiles, vitamin C is made in the kidneys, but in mammals, production has been transferred to a much larger organ, the liver. During the age of prosimians, however, a mutation occurred in primates, that deleted the enzyme L-gulono-oxidase, which is necessary for vitamin C synthesis (Scrimshaw and Young, 1976). Of mammals other than primates, only bats and guinea pigs are known to lack the ability to synthesize vitamin C.

Unable to synthesize vitamin C, primates must acquire it through food. In the absence of suitable food, a deficiency of vitamin C causes the disease called scurvy. Although chimpanzees and monkeys are known to develop scurvy, the artificial diets of captive breeding programs are the cause. In conditions where wild food is normally taken, the development of scurvy seems impossible. G. H. Bourne (1949, 1971) of the Yerkes Pri-

mate Research Center estimates that the intake of vitamin C by wild chimpanzees reaches 4,500 mg/day. In humans, who are larger-bodied than chimpanzees, 20 mg/day is sufficient to resist scurvy.

Recently, researchers have hotly debated the medicinal effects of vitamin C use. The effect of vitamin C on the body is not merely a passive prevention of scurvy, but instead it has a broad connection with the maintenance and promotion of good health. As a result, a far larger quantity of vitamin C than the current intake standard may be needed for good health (the current standard differs depending on the country, 20–75 mg/day). The basis of this view is the supposition that animals who can synthesize vitamin C, and certainly primates who cannot synthesize it, consume and use 1 g of vitamin C per day.

The above argument was examined for wild pygmy chimpanzees, who are frugivores, and two predictions were made. First, the fruits and leaves eaten by pygmy chimpanzees will have higher concentrations of vitamin C than those not eaten; that is, the pygmy chimpanzee gathers vitamin C very efficiently. Second, the total amount of vitamin C available in consumed natural foods will far exceed the minimum requirement, and will amount to the several grams per day previously suggested by Bourne.

Because vitamin C is easily destroyed, the analysis of sample material must be limited to fresh items, preferably analyzed on the spot. I approached Ryu Asato, of the Laboratory of Nutritional Studies of Ryukyus University, who agreed to participate in an on-the-spot investigation. With a large quantity of his test equipment and reagents, we rode into Wamba to conduct the first on-the-spot analysis of vitamin C in primate field research.

Batofe fruit was the first to be analyzed. At the time, it was a very important food item showing an intake ratio of close to 100%. The results of the test, however, showed unexpectedly that the vitamin C content was *zero*. Dissatisfied, I asked about the analysis, and Asato said he had used fruits provided by villagers four or five days before, when test preparations were not yet ready. I protested that there was a problem in the samples, and then instructed some villagers to climb trees and gather fresh fruits. This time, vitamin C was detected, but at only 1.2 mg/100 g of edible part, which is a low level, 1/20 to 1/60 that of sweet oranges and 1/65 that of papaya (oranges and papayas were analyzed at about the same time). In the end, however, this was the highest value obtained for *batofe*. Results of later tests, repeated several times, all remained in a range of 0.5–1.0 mg (average, 0.7 mg) per 100 g of edible fruit.

When the *batofe* trees stopped producing, *Dialium* (*elimilimi* and *keke*), followed by *ntende*, became the most important food items. They showed a higher vitamin C content than *batofe*, with an approximate average of 3.7 mg % (3.7 mg/100 g) and 4.7 mg %, respectively; but even so, compared with other fruit, it was never high.

In addition to the above-mentioned important fruits, about 50 kinds of pygmy chimpanzee foods have been analyzed for vitamin C. Among fruits, only *bolengalenga* (a fruit of *Cissus* spp., woody vines) showed an exceptionally high value of 30 mg %. Others generally do not reach 10 mg %, and as a rule, vitamin C content was low compared to that of human cultivated foods. Thus, the first prediction, that pygmy chimpanzees would take foods high in vitamin C, was not borne out.

The second prediction was that the total quantitative intake of vitamin C would be high. In order to determine the amount of vitamin C taken in, we must first determine the respective quantities of the different foods consumed. Because this is impossible at the present stage of research, we must use indirect methods to obtain approximate values.

A starting point is to calculate the basal metabolic rate, which for animals is given in the formula $BMR = 70 \times W^{0.075}$ kcal/day, where W is the weight (kg) of the animal. No wild pygmy chimpanzee has been weighed, however, so we shall use 35 kg, which is roughly 85% of 40 kg, the highest value for an adult common chimpanzee at Gombe Park. If this 35 kg value is used as the maximum weight of a wild pygmy chimpanzee, the BMR comes to 1007 kcal/day.

Animals bred in the zoo do best if they consume calories at twice the BMR, and many researchers suggest a value of three times BMR for animals in the wild. If we take the latter as our model and use 35 kg as the weight of the pygmy chimpanzees at Wamba, we calculate that 3021 kcal/day of energy are being consumed. On the basis of A. G. Goodall's (1977) nutritional analysis of wild gorillas, 100 g dry weight of a sample portion of wild fruit yields an average of 540 kcal (gross calories). Because indigestion and other losses average 46%, the actual rate of ingestion is 289 kcal per 100 g dry weight of fruit. Thus, when only wild foods are used for food, the pygmy chimpanzees of Wamba need 1045 g/day in dry weight.

Using 1045 g/day as a base value, when only *batofe* is eaten, the intake of vitamin C per day is 25 mg; when *Dialium*, 58 mg; and when *ntende*, 309 mg. Thus, vitamin C intake from these major foods is expected to be much less than the 4,500 mg estimated by Bourne (1949, 1971). Only when pygmy chimpanzees eat the fruit of *bolengalenga*, which

has an exceptionally high vitamin C content, does the intake per day barely reach 1,200 mg.

Certainly, the calculated value of vitamin C intake depends on the food species, the ingestion (absorption) efficiency, the body size of the animal, and the multiple of the BMR used to calculate the number of calories needed per day under natural conditions. However, wild pygmy chimpanzees are unlikely to consume 10 or 20 times their BMR and, therefore, the amount of vitamin C ingested by a pygmy chimpanzee is likely to be limited to several tens to several hundreds of milligrams per day when feeding on its usual natural foods. The number of days that a pygmy chimpanzee ingests vitamin C at the gram level, if any, is very small, perhaps only several days per year. On the basis of our study of the pygmy chimpanzees at Wamba, we do not agree with Bourne's estimate that more than 4 g per day are normally ingested.

Vitamin C reaches saturation at 1–1.7 mg/kg of body weight. The level of vitamin C intake in pygmy chimpanzees may be sufficient to reach saturation, but does not greatly exceed that level, presumably because there is no need. The defect in vitamin C synthesis that occurred at the level of prosimians was not a grave mutation, because the resulting deficiency could be easily cured by regularly ingesting fresh plant food. Special food habits that selected for foods high in vitamin C were not needed, thus allowing the lineage of primates that had a genetic vitamin C deficiency to achieve the colorful radiation seen today.

Protein. Protein often is a problem in the nutrition of primates, which are plant eaters. On the basis of Asato's analysis, calculating protein content by the same method used to evaluate vitamin C content, the estimated amount of crude protein was 29, 49, and 59 g/day, for the consumption of *batofe*, *Dialium*, and *ntende*, respectively. Because the amount of protein necessary for good health is 1 g/day/kg body weight, protein intake was above the required level for each of the three staple foods.

In general, such plant parts as leaves, pith, and stems have a higher protein content than the flesh of fruits (Table 13). As a consequence, the fiber-eating gorilla has an easier time acquiring protein than does the frugivorous pygmy chimpanzee. According to A. G. Goodall (1977), the Kahuzi gorillas take, from vegetables alone, three to six times the daily requirement of protein. The consumption by pygmy chimpanzees of fibrous foods every day, even when fruits are abundant, may be required to supply the necessary amount of protein.

Table 13. Amount of vitamin C and crude protein (fresh weight) per 100 g of food (from Asato's unpublished analysis)

Food	Vernacular name	Plant part	Water content (%)	Protein (%)	Vitamin C (%)
Fruits					
Landolphia owariensis	*batofe*	pulp	71.4	0.8	0.7
Mammea africana	*bokoli*	pulp	64.4	2.8	2.5
Cissus myriantha	*bolengalenga*	pulp	73.9	1.5	30.3
Croton haumanianus	*bonyanga*	pulp	74.5	2.8	3.8
Uapaca guineensis	*bosenge*	pulp	92.4	0.2	1.1
Dialium zenkeri	*elimilimi*	pulp	32.4	3.8	4.0
Dialium corbisieri	*keke*	pulp	34.0	2.6	3.3
Aframomum laurentii	*ndake*	pulp	96.1	0.2	4.0
Pancovia laurentii	*tende*	pulp	84.1	0.9	4.7
Beans					
Afzelia bipindensis	*bala*	bean	70.2	6.6	2.5
Anthonotha fragrans	*boppembe*	bean	38.0	6.1	0.4
Anthonotha macrophylla	*lomuma*	bean	45.2	5.1	1.3
Fibrous food					
Megaphrynium macrostachyum	*beiya*	shoot	88.9	4.2	8.3
Haumania liebrechtsiana	*bokombe*	shoot	90.4	3.2	1.8
Aframomum laurentii	*bosomboko*	pith	70.0	3.1	3.8
Leonardoxa romii	*bokumbo*	young leaf	75.0	3.4	7.3
Manniophytom fulvum	*lokosa*	young leaf	75.0	4.3	37.6
Palisota ambigua	*liteletele*	stem	79.2	4.0	2.7
Ancistrophyllum secundiflorum	*bokau*	pith	88.9	3.0	2.2
Cultivated fruit					
Ananas comosus	pineapple	pulp	84.9	0.4	14.1
Musa sapientum	banana	pulp	73.8	1.3	3.0
Carica papaya	papaya	pulp	86.4	0.7	79.2
Persea americana	avocado	pulp	83.9	1.2	7.1
Citrus sp.	A			0.0	70.3
Citrus sp.	B			0.0	28.1
Citrus sp.	C			0.0	29.5

The intake of animal protein seems generally to make only a trivial contribution to the nutrition of the pygmy chimpanzees of Wamba. The one exception is the larvae of the skipper butterfly (*tohilihili*). On average, one pygmy chimpanzee consumed approximately 200 caterpillars during each feeding bout, averaging 18 minutes. This feeding bout amounts to a fresh weight of approximately 100 g, which converts to 7.5 g of crude protein. Because the chimpanzees feed, on average, three times a day throughout the season, the calculated total quantity of crude protein

for a day was 22.5 g, more than 60% of the protein required by a 35 kg adult. Although this value represents a meaningful contribution to nutrition, the food season of butterfly larvae ends after only a short time.

Grass-eating ruminants such as cows have a symbiotic relationship with protozoans living inside the alimentary canal. Hideo Hasegawa of Ryụkyus University School of Medicine's Laboratory of Parasitology kindly allowed me to bring to him for analysis several hundred pygmy chimpanzee fecal samples from Wamba. He discovered in the feces a huge number of protozoans, along with eggs of various parasites. Because the protozoans were so big and their numbers so great, Hasegawa at first thought they were food fragments. I wonder if these protozoans have a symbiotic relationship with pygmy chimpanzees, but this is a problem for future examination.

Comparison with Common Chimpanzees

The number of common chimpanzee foods reported at Mahale, already 205 plant food items in 1974, presently amounts to 300 items. R. W. Wrangham (1977) reported 140 items at Gombe Park on the basis of two years of research, but the number exceeds 200 items when his observations are combined with those of other researchers. In the Ipassa Forest of West Africa, C. M. Hladik (1977) identified 174 items in one year, but if we include those things that are not yet identified, the number of items is 318. At Wamba, 147 food items of pygmy chimpanzees have been identified during research spanning ten years; this number is less than for common chimpanzees at any of the three above-mentioned regions.

Because differences in observation conditions or periods can bias data, it is dangerous to assert unequivocally that the common chimpanzee exploits a greater diversity of foods than the pygmy chimpanzee. Nevertheless, the tropical rain forest of Wamba is far richer and more complicated in floristic composition than the drier vegetation of Mahale and Gombe. Given the differences in the extent of food resources they can use, pygmy chimpanzees seem to use a relatively smaller portion than common chimpanzees.

A comparison of the number of food types eaten per month, as well as per day, also suggests that the common chimpanzee uses a greater diversity of foods than the pygmy chimpanzee. According to Wrangham (1977), 14.6 species per day and 60 species of food per month are consumed by common chimpanzees at Gombe Park. Hladik (1977) reports that an average of 20 kinds of food are used in one day by common chim-

panzees in the Ipassa Forest. Both are higher values than those obtained for pygmy chimpanzees at Wamba.

Food items, consisting of fruits, seeds, leaves, pith, bark, and various animal foods, are conspicuously similar in both species of chimpanzee. Among these items the proportion occupied by fruit (including seeds) in pygmy chimpanzees is 57% at Wamba, 63% at Yalosidi, 57% at Lomako, and in general, about 60%. In the common chimpanzee at Mahale, it is 34%, which is high when compared to the 6–10% of the gorilla, a fibrous-food eater, but low when compared to the pygmy chimpanzee.

Chimpanzees have been thought to be mainly frugivorous. Because fruit constitutes 80–90% of the diet at Wamba, estimated from the proportion of time spent feeding and from fecal analysis, pygmy chimpanzees are true to their reputation. In the common chimpanzee, however, the proportion of consumed foods differs somewhat from one site to another. At Gombe, the ratio of consumption according to feeding time was 47.1% fruits; about 32.0% leaves and bark; and 20.9% larvae and other material (Teleki, 1981). At Ipassa Forest, the proportion of fruit was still lower, a mere 14.4%, whereas the proportions of leaves and animals (larvae) were 48.8% and 36.8%, respectively (Hladik, 1977). At Mahale, the proportions of plant foods were calculated for two groups: fruits constituted 73–95% of the food eaten during one month by M-group and 7–47% of the food eaten by K-group (Nishida, 1974). Fruits comprised 90%, and other foods 10%, of the diet of common chimpanzees in the Budongo Forest (Reynolds and Reynolds, 1965).

Although there are exceptional cases such as the Mahale M-group and the Budongo Forest residents, in general, the importance of fruits in the diet of the common chimpanzee is lower than in the pygmy chimpanzee. Conversely, fibrous and animal foods are consumed in higher proportions by the common chimpanzee. In fact, a special characteristic of the common chimpanzee is that it ordinarily consumes animal food in notable quantities. A common chimpanzee at Gombe eats an average of 10 g of meat in one day and, in addition, may consume many invertebrates (Hladik, 1977). The chimpanzees at Mahale frequently feed on ants and also prey upon vertebrates; in 1981, 37 examples of meat eating were reported (Takahata, Hasegawa, and Nishida, 1984). It was also reported that the total time spent feeding on animal food amounted to 4% at Ipassa Forest. Compared to this, consumption of animal food at Wamba is extremely meager, amounting to no more than 1% of the total by fecal analysis and 1.5% by direct observations.

As previously stated, regional, group, and individual differences

occur in the pygmy chimpanzee diet, and are well documented for the common chimpanzee also. Probing into such dietetic differences at various levels may provide clues to the flexibility of the chimpanzees' food habits, in particular how they can change their food customs in response to environmental changes. Such probing may also help us to assess their food culture, in particular how they pass on their food customs from group to group, or change them from region to region. Presently, however, the data on regional, group, and individual differences are insufficient to compare the two species of chimpanzee.

One criterion for evaluating the plasticity of food habits is the ability to accept new kinds of food. The common chimpanzee eats many cultivated plants, among them sugarcane, papaya, sweet orange, and pineapple. Oil palm fruits are eaten by the common chimpanzees of West Africa and East Africa. Although the oil palm was brought to East Africa by way of Zaire, and thus must have an older history in Zaire, we have not yet observed pygmy chimpanzees using oil palms. The common chimpanzee may have the greater ability to accept new foods.

When comparing the food habits of the two chimpanzee species, we find that the common chimpanzee uses the habitat more intensely. It obtains a greater diversity of foods and is more progressive in acquiring new foods. That is, the common chimpanzee has a higher ability to exploit food. On the other hand, the pygmy chimpanzee consumes more fruit than the common chimpanzee.

Here, we must also consider the differences in food habits between the common chimpanzees of Mahale's M-group and K-group. Each group had a large, suitable, home range that overlapped the other in the Kasoge Forest. When M-group entered, however, K-group took shelter in the woodland belt (Nishida and Kawanaka, 1972). The proportion of fruits in the diet was high in M-group but low in K-group, perhaps the result of M-group's monopolization of preferred habitat. The proportion of fruits in the diet of common chimpanzees of the Budongo Forest is exceptionally high, but this region is known to be one of the highest density areas for the common chimpanzee.

The proportion of fruit in the diet becomes a point of speculation about the stability of diets. The pygmy chimpanzee, with its diet proportionately high in fruits, may have been in a stable food environment throughout its history. Conversely, the common chimpanzee, which is situated in a more diverse and unstable, severe environment, has developed a greater ability to exploit its food resources.

CHAPTER FIVE

Behavior of Individuals

Daytime Behavior

Although Wamba is situated directly on the equator, the exact times of sunrise and sunset vary by about 30 minutes during three months of the year. Coping with this time variation, pygmy chimpanzees leave their nests at between 5:20 and 6:20 A.M. and make their nests at night between 4:45 and 5:45 P.M. That is, the pygmy chimpanzees rise on average about 30 minutes after sunrise and retire about 40 minutes before sunset. The intervening 11.5 hours comprise the pygmy chimpanzee's daytime active period.

Because the pygmy chimpanzees live deep in the forest, they get up and go to bed in dim light. On mornings when there is rain or dense fog, they get up later, and after heavy rains they tend to retire early.

The daily activities of the pygmy chimpanzee are divided into six categories: feeding in the trees, rest, travel, foraging, nest-building, and group excitement. Because following individuals was inefficient, I based this classification on the movements of the whole party.

Arboreal feeding. During arboreal feeding, most members of a party are feeding in the trees. During the first 10 to 20 minutes after arriving at a feeding tree, chimpanzees feed excitedly and enthusiastically. Gradually, they calm down, become languid, and finally rest, but since behavior continually changes, clear boundaries between feeding and rest are difficult to observe.

Rest. During rests, most members of the party are inactive in the trees and on the ground or are indulging in characteristic rest-time friendly behaviors such as grooming or play. They also often make nests and nap. Seldom are all members resting at the same time; usually two or three individuals feed intermittently.

Travel. After a rest, one of the pygmy chimpanzees emits a "waa waa" in a loud voice, and the others cheer in chorus. This long distance call occurs intermittently, while the number of chorusing individuals increases. The party descends to the ground and the number of individuals displaying "branch-dragging" behavior increases. The choruses and displays increase in frequency, and pave the way for the forthcoming group-travel.

Following the last chorus, travel begins. Individuals who had been napping rush out from their nests. Individuals who had been grooming run several meters while shouting and then sit down. Then after a short rest, all at once, all of the members of the group begin to move, descending silently to the ground.

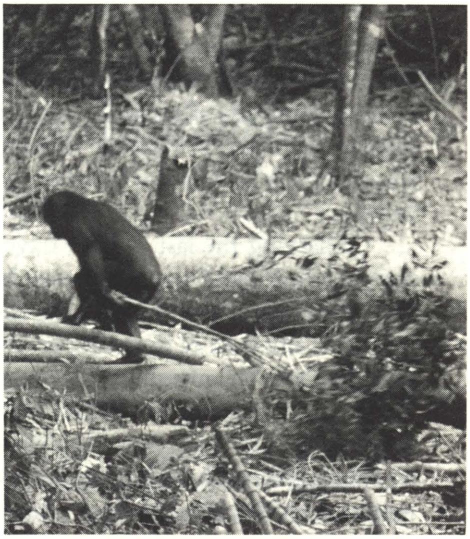
Pygmy chimpanzees usually travel silently on the ground until they arrive at the next food tree. Upon arrival, a loud chorus erupts, but while en route, not much vocalizing occurs. They usually cover a few hundred meters at a time, but on rare occasion they can travel as much as 2 or 3 km at a time.

Foraging. In the activity categorized as travel, definite direction and orderly movement are seen. Pygmy chimpanzees, however, frequently also travel very leisurely, without closely coordinated movements. One individual searches for food; another is absorbed in grooming and play; and another sits idly, or lies sprawled on the ground or in a tree close to the ground. The whole party, however, is slowly moving. For the moment, I am calling this type of group activity "foraging," which includes opportunistic feeding, moving, resting, and social activities. While foraging, the party is widely spread out, with the distance between the head and the tail of the party sometimes reaching 500 m.

Nest-building. In the daytime, party members build nests at different times according to personal preferences, but at night, all of the party members build nests more or less simultaneously. Upon arrival at their sleeping site, the chimpanzees, all at once, begin to climb the trees, and while giving the long distance call, begin to build their nests. No matter how large the party, all individuals finish making their nests, simultaneously, in 15 to 20 minutes.

Group excitement. There are various situations when the whole party enters into an excited state: when the chorus of a different party is heard; when a new party joins; or when a member of another unit group approaches. During group excitement, pygmy chimpanzees cry loudly,

A group at rest in the trees.



A pygmy chimpanzee dragging a branch.

Pygmy chimpanzees all moving in one direction.

scream in shrill voices, and run around in the trees and on the ground. They drag branches, and aggressive, reassurance, and sexual behaviors occur extensively. This state of excitement usually ends after ten minutes, but once in a while, it may last for half an hour or even an hour.

The daily activity of the pygmy chimpanzee consists of a cycle of resting, travel, feeding, and resting. The peak feeding hours are in the early morning, but when foods are not abundant, travel and food-gathering behaviors merge and become foraging behavior. After a second feeding peak in the late afternoon, the chimpanzees return to foraging, or to a combination of feeding and resting, and begin to travel toward the nest-building site.

The percentages of time spent in the various daily activities are, in order, 43% resting, 20% foraging, 20% feeding in the trees, 13% travel, and 13% other. Because some time spent on feeding is also included within the foraging category, I estimate that the time that pygmy chimpanzees spend feeding exceeds 20%, but does not exceed 30%, of the daily activity time.

Daily Travel Distance and Home Range

Our pursuit of pygmy chimpanzees begins upon arrival at their sleeping site before they have left their nests. Although they are easily followed while feeding in the trees, when they descend to the ground and begin to travel or forage, following them becomes difficult since they make few vocalizations on the ground. Nevertheless, as the evening nest-building time approaches, we can determine where they are from their many loud choruses.

Although following a party throughout the day is difficult, we note on a map the confirmed places from which the chimpanzees left their nests and the places where they made their sleeping beds at the end of the day. By rounding the distance covered in traveling and foraging to the nearest tenth of a kilometer (joining the points with a gently sloping curve), I determined that the median distance traveled during a day was 2.0 km (range, 0.4–6.0 km).

Most researchers would predict that the daily travel distance would be short when food was abundant and would increase during periods of food shortage. Although I observed this tendency, travel distances were not significantly different between food seasons. Differences in party size, however, were observed depending on the fruit season. When preferred foods were abundant, pygmy chimpanzees formed large parties.

During shortages between fruiting seasons, they tended to split into smaller parties. The ability to freely change party size, by the fission-fusion process, must have been adaptive since it enables effective use of food resources.

Until 1982, the reported home range of Wamba's E-group was 58 km^2. Of that total, however, 66% overlaps home ranges used by other unit groups. Some regions are even jointly held by three unit groups. The joint ownership of influential food resources by several groups is a distinctive feature of pygmy chimpanzees.

Because parts of primate home ranges are commonly used jointly by several groups of the same species, group home ranges are often divided into overlapping parts and a core area. The core area belongs exclusively to one group and includes several prominent food areas in which other groups are absolutely forbidden to trespass. The territory monopolized by Wamba's E-group, however, contains roads dotted with hamlets and consists of cultivated land and fallow secondary bush. As a food source, it is the least valuable part of E-group's habitat and it may be monopolized by E-group merely because the other groups neglect it.

Group ranges are not static. As the E_1 and E_2 subgroups have been drifting apart, so have the ranges of both groups gradually changed. At first, from 1980 to 1981, the E_1 subgroup extended its range to the west, resulting in an increase of the overlapping area with P-group. Moreover, starting in about 1983, the E_1 subgroup extended its range to the southeast, penetrating more than 1 km into the monopolized region of B-group. In the region of overlap is the swamp forest of *Uapaca*, a vast food zone that the E_1 subgroup now shares with B-group. Since 1981, the E_2 subgroup has extended its range to the north and northwest, and it travels southward into the range of the E_1 subgroup less and less frequently.

Habitat Utilization

As previously discussed, the vegetation of the Wamba region is generally classified into five types: dry primary forest, swamp forest, old and young secondary forest, and secondary bush (cultivated and fallow land). Table 14 is a summary of the rate at which pygmy chimpanzees use each vegetation type—that is, the number of days each vegetation type was used relative to the total number of days in the study, and expressed as a percentage.

Dry primary forest had the largest proportionate use, reaching 93.5% and indicating that it is the most important vegetation for the pygmy chimpanzee. The majority of the pygmy chimpanzee's principal

Table 14. Utilization of vegetation types (Kano and Mulavwa, 1984)

	Proportion of utilization in % (number of days used/number of days observed)				
Vegetation type	Dry primary forest	Swamp forest	Aged secondary forest	Young secondary forest and bush	Number of days
Landolphia owariensis	93.5	37.1	54.8	8.1	62
Transitional	100.0	50.0	50.0	0	2
Other Apocynaceae spp.	100.0	41.9	48.4	19.4	31
Transitional	100.0	12.5	43.8	31.2	16
Dialium sp.	97.1	42.9	20.0	31.4	35
Transitional	81.8	18.2	63.6	45.5	11
Pancovia laurentii	84.0	12.0	52.0	20.0	25
Transitional	77.8	11.1	55.6	11.1	9
Undetermined	100.0	25.0	62.5	37.5	8
Total	93.5	31.2	47.2	20.6	199

foods are produced in this vegetation type. Old secondary forest (47.2%) ranks second. Several important foods such as *batofe* (a fruit representative of the family Apocynaceae) and *ntende* (*Pancovia laurentii*, Sapindaceae) are produced both in primary forest and in old secondary forest. Herbs (Marantaceae), which constitute the bulk of fibrous foods, grow mainly in old secondary and dry primary forests.

The utilization rate of the swamp forest was 31%. The data collected in 1981 did not include the principal foods from the swamp forest, but in the latter half of December 1984, the principal species *bosenge-alosi* (*Uapaca hendelotii*) bore a large quantity of fruit in the swamp forest of the Luo River. The movement of the E_1 subgroup reflects dependency on that fruit for a full month. In addition to *bosenge-alosi*, several foods were seen in abundance in the swamp forest, such as the shoots of *mpeto* (*Sclerosperma mannii*), a species of Palmae, and African ginger (*Aframomum* sp.).

The utilization rate of young secondary forest and secondary bush was lower, averaging 21%. The utilization rate rose (31% to 46%) just before and after the *Dialium* season, when the fruit of the parasol tree (*Musanga smithii*) and the fruit and pith of African ginger were eaten. Chimpanzees are able to utilize these non-seasonal foods throughout the whole year and, in times of food shortage, their relative importance rises.

Quantitative data concerning the utilization of habitats across the vertical dimension have not been obtained. Nevertheless, because the overwhelming majority of principal fruits are produced in the forest crown, pygmy chimpanzees probably spend the highest proportion of

Table 15. Primates inhabiting the forests of Wamba

Common name	Vernacular name	Scientific name
Potto	*kachu*	*Perodicticus potto*
Bushbaby	*lisire*	*Galago demidovii*
Red-tailed monkey	*soli*	*Cercopithecus ascanius*
Mona monkey	*beka*	*Cercopithecus mona*
DeBrazza monkey	*punga*	*Cercopithecus neglectus*
Blue monkey (?)	*ikese*	*Cercopithecus mitis* (?)
(none given)	*ekele*	*Cercopithecus salongo*
Guenon	*tolu*	*Cercopithecus* sp.
Red colobus monkey	*yemba*	*Colobus badius*
Angolan colobus	*luka*	*Colobus angolensis*
Black mangabey	*gila*	*Cercocebus aterrimus*
Allen monkey	*elenga*	*Allenopithecus nigroviridis*
Pygmy chimpanzee	*elia*	*Pan paniscus*

their time in the upper tree layer. Some fruits (e.g., *ntende*) are also produced in medium-size trees. In the lower stratum, food production is poorest. Here, many trees do not produce fruits because they are saplings, and trees that do have edible fruits produce scantily. In search of food, the pygmy chimpanzee even extends its activities to the subterranean level, by digging earthworms, and into streams and swamp beds.

Many species of primates in addition to the pygmy chimpanzee have been observed at Wamba, and Table 15 lists them all. Although their habits have not been examined in detail, we believe that no other primate species uses such diverse food types and strata as the pygmy chimpanzee. For example, *Cercopithecus ascanius* occupies and is the master of the dry primary forest, leaving occasionally for secondary forest. The black and white colobus occupies the deepest part of the dry primary forest, and red colobus and DeBrazza monkeys are confined to the swamp forest. Compared with these sympatric primate species, the pygmy chimpanzee has the widest niche.

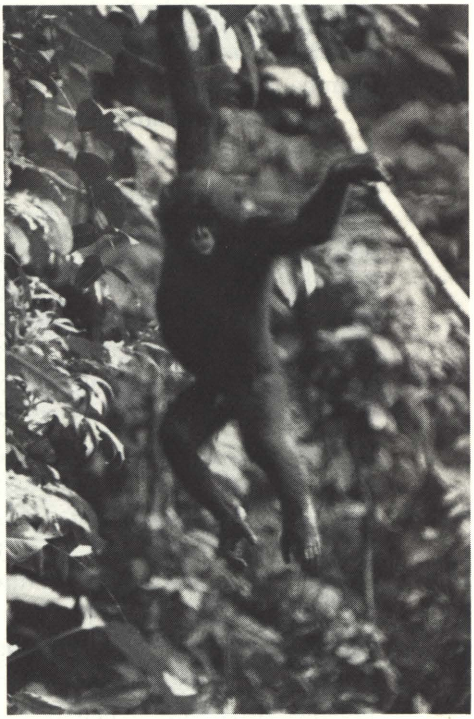
Searching for Food

Although a pygmy chimpanzee finds food at all levels of the forest, the principal source of nourishment is found at heights of 25 to 40 m above the ground. The feeding behavior of pygmy chimpanzees in trees occurs in three stages. First, a pygmy chimpanzee—let us say a male—climbs the tree to reach the food. Second, he gathers, transports, and ingests the food while remaining in the tree. Third, he descends the tree.

When the chimpanzee climbs a tall tree, which may have a diameter of more than 50 cm, he avoids a direct ascent, perhaps by using a vine dangling from a branch or twining around the tree trunk. When there is no suitable vine, he will use an adjacent narrower tree trunk to reach a bough of the taller food tree.

When climbing up, the chimpanzee's limbs move in the order right hand, left foot, left hand, right foot. The second through fifth fingers, which are very long, are used to hook or to clasp the substrate supporting the suspended body. The arms seem to be more propulsive than the legs, which are bent a little at the knee while climbing. If the substrate is thick, the feet extend to get a firm hold. If the substrate is narrow, they hold it lightly between the big toe and the other four toes, or, depending on the circumstances, they may clasp the substrate firmly. In this way, the position and movement of the foot against the substrate are similar to those

A pygmy chimpanzee climbing a slender vine, with an infant at its loins.



A branch bends under the weight of a young male pygmy chimpanzee as he brachiates, or arm-swings.

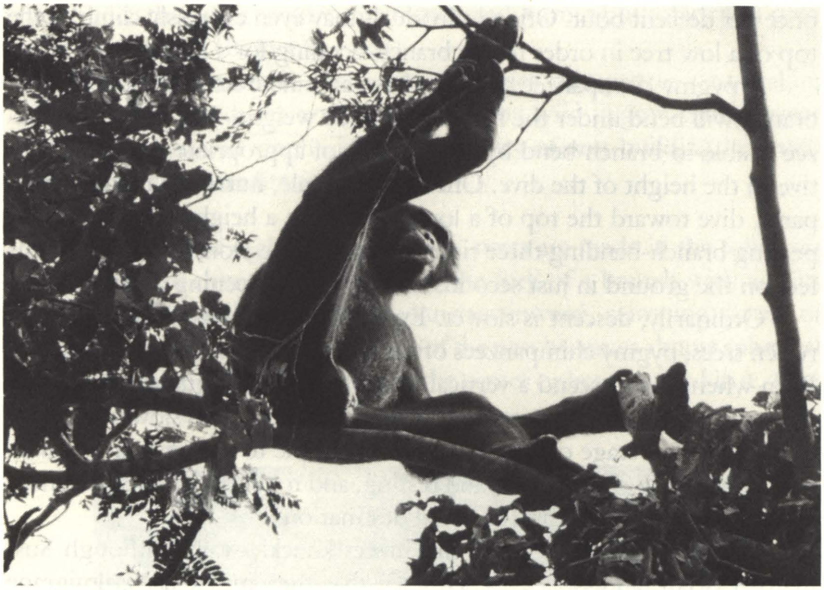
employed during horizontal movement in a tree. The ventral surface of the body does not contact the substrate.

Fruit is usually found at the surface of the forest crown, but the small branches at the tips cannot possibly support the weight of a pygmy chimpanzee. Consequently, when one walks along a big branch toward the tip, he or she stops just before a dangerous place, extends an arm, bends the branch, pulls it in, and removes the food. Also exhibited is a unique suspensory motion in which the body weight is dispersed by grasping at least two separate branches with the hands and feet. Then, before the branch breaks, the pygmy chimpanzee moves from branch to branch to alter the center of gravity, and approaches the food in the surface of the crown.

Pygmy chimpanzees eat only where they have a firm hold on the substrate. Therefore, they may have to carry the food a short distance. Pygmy chimpanzees usually carry food in their hands, but they also use their mouth or foot, though less frequently. Sometimes, they carry twigs or sugarcane in their inguinal region, a method first described by Jane Goodall as the "groin pocket" in the common chimpanzees at Gombe. At Wamba, certain individuals use it frequently, while others never do.

Pygmy chimpanzees usually sit when ingesting food. They sit most frequently with the soles of both feet on the substrate, a branch, and the buttocks or the base of the thigh on the same or another substrate. When the branch is slender, they contact the substrate only with their feet, and squat. Occasionally, they loosely dangle both legs while sitting on a branch, and they also bring food to their mouth while hanging by one hand. Although every imaginable variation occurs in sitting positions while eating, pygmy chimpanzees only occasionally eat while lying sprawled or standing quadrupedally, tripedally, or bipedally.

After feeding, pygmy chimpanzees rest and then descend to the ground to travel. When ascending to a feeding spot, they move up almost vertically, but when descending to the ground, they move diagonally. The average horizontal distance between the take-off point and the landing spot is 10 to 50 m. This horizontal displacement is related to their descent technique, branch-bending, which occurs whether they are moving quadrupedally or by brachiating. When a pygmy chimpanzee moves toward a branch tip, the branch bends because of his body weight, and he descends naturally. At the same time, the gap between him and the neighboring tree narrows. When the gap is still large, however, he may brachiate or leap across to the neighboring tree. Although pygmy chimpanzees will often descend using vines or trees, branch-bending is usually used at least



A male sitting and feeding on a *batofe* fruit.

It is not unusual to see a pygmy chimpanzee walk bipedally over a distance of 20 m while carrying sugarcane.

once per descent bout. Often individuals may even expressly climb to the top of a low tree in order to use branch-bending for a descent.

A pygmy chimpanzee seems to have an innate sense of how much a branch will bend under the force of its body weight. A pygmy chimpanzee is able to branch-bend by using a tree of appropriate thickness relative to the height of the dive. Once I saw a male, hurriedly following his party, dive toward the top of a lower tree from a height of 50 m. By repeating branch-bending three times in rapid succession, he landed on his feet on the ground in just seconds. It was an eye-opening aerial show.

Ordinarily, descent is slower. Especially before traversing a gap between trees, pygmy chimpanzees often take short rests of several seconds. Even when they descend a vertical tree trunk, they frequently come to a stop, still in descending posture, to take a short rest. This slow movement during the first stage of travel may provide time to gather relatives who had dispersed during feeding and resting, and to reach a silent agreement about the party's next direction and destination.

On the ground, pygmy chimpanzees knuckle-walk. Although Susman, Badrian, and Badrian (1980) say that they might use palmigrade walking (with the fingers spread and the palm down) in the mud of the swamp forest and in streams, I have always observed them knuckle-walking when on the ground, whether in a stream or on the forest floor. When they search for food on the ground, they may not need a high level of locomotor skill. They never use tools such as a piece of wood, and even when digging for worms, they only use their hands.

The branch-dragging behavior that occurs often on the ground is a special kind of locomotor behavior in which a pygmy chimpanzee moves in a tripedal run; the arm carrying the branch is slightly bent and held in the air. Less frequently, pygmy chimpanzees drag branches bipedally or quadrupedally with the branch in their mouth. They often move quadrupedally when carrying sugarcane in a hand or foot; they rarely carry it in the groin pocket or in their mouth.

Nest-Making

Nest-making behavior is common to all large-bodied apes. Under wild conditions, almost all individuals build nests in the evening and rest there at night. According to laboratory research, even zoo-bred chimpanzees who have never seen a nest will usually make something like one when given appropriate materials. They are never able, however, to make a complete one. Although chimpanzees have a natural disposition to

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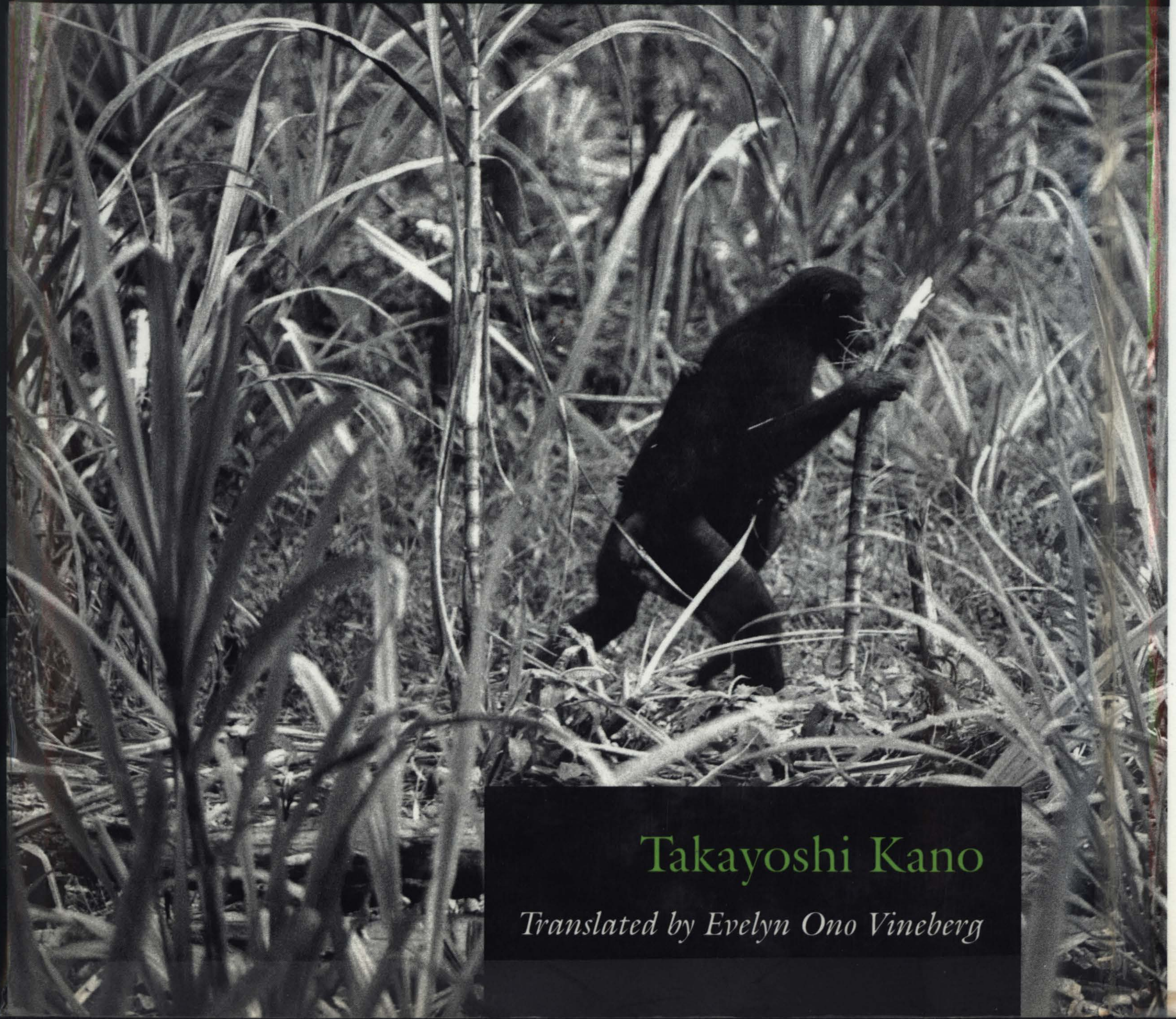

Takayoshi Kano

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The Last Ape

Pygmy Chimpanzee Behavior and Ecology

TAKAYOSHI KANO

Translated by
Evelyn Ono Vineberg

Written by one of the world's principal specialists on the pygmy chimpanzee, this is the first comprehensive work on the last of the African great apes to be studied in the wild. Also the rarest of the great apes, it is found only in the tropical forest region of central Zaire. The Wamba Forest is the site of the longest continuous field study of the pygmy chimpanzee, and this book is a richly illustrated, first-hand account of the author's observations and experiences in Wamba from 1974 to 1985.

The pygmy chimpanzee differs taxonomically and physiologically from the familiar "common" chimpanzee seen in zoos and circuses. It is smaller, darker, and slimmer, stands more upright, and is far more active sexually throughout its life. There are also great differences in its behavior and its social and ecological relationships. Throughout, the author compares the two species, giving the reader an appreciation of their contrasting habits.

Pygmy chimpanzees are thought by some to be the closest living relatives to

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(continued from front flap)

ancestral *Homo sapiens*. As such, they are broadening our understanding of human and prehominid evolution. On the basis of individual survival, they are the most successful of the higher primates. In most primates, "competition" determines how individuals and groups subsist and leave descendants, and dominate or subordinate rank determines relationships between individuals. But by pursuing sexual and quasi-sexual behavior during interactions—between individuals of any age or sex and with remarkable frequency—pygmy chimpanzees conceal the operation of rank and live peacefully together in large groups. Their sexual behavior also promotes food sharing, reduces tensions between males and females, and indeed matches our own in complexity and bonding importance.

After the first chapter, "Why Study Chimpanzees?," the author presents chapters on distribution, social groups and social patterns, food, the behavior of individuals, sexual behavior, and social behavior and social relationships. He concludes with a summary chapter, "Why Are Pygmy Chimpanzees Interesting?"

The book includes 8 maps and 78 striking photographs that depict the wide behavioral repertoire of the pygmy chimpanzee.

Takayoshi Kano is Professor of Zoology at the Primate Research Institute, Kyoto University.

Marmots

Social Behavior and Ecology

David P. Barash

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—Gail R. Michener, *Science*

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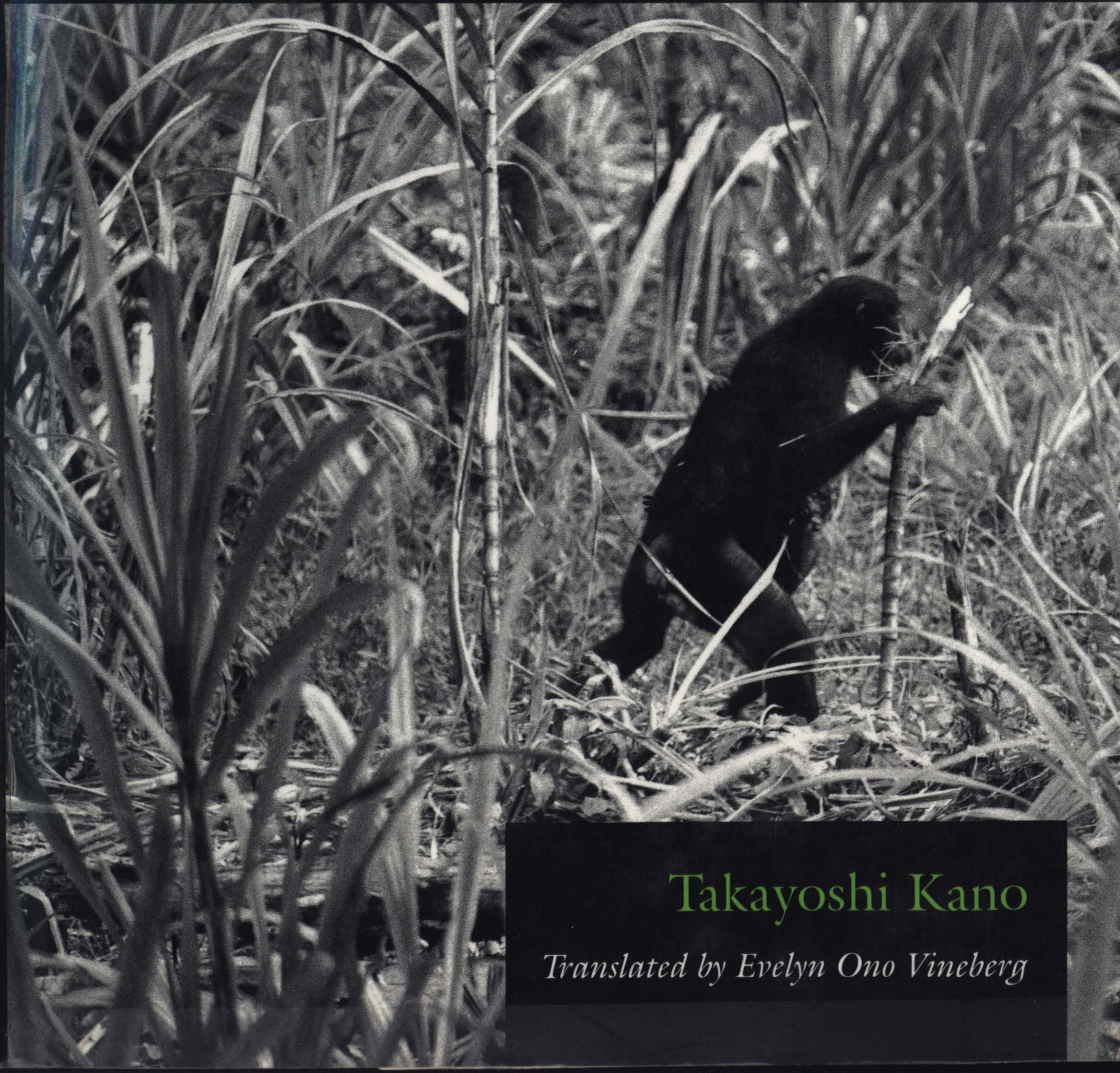

Takayoshi Kano

Translated by Evelyn Ono Vineberg